VERTEBRATE FOSSIL COLLECTIONS—A FRAGMENTARY DOCUMENT

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The fossil record plays a unique role in the study of biology, for it provides our only appreciable access to the time dimension of evolution as an historical process. To expatiate momentarily upon the obvious, the most nearly universal characteristic of the fossil record is the fact that it is fragmentary. The causes of this fragmentary nature—structure and mode of life of plant or animal, age, and pure chance—also introduce a bias into the fossil record. We need not concern ourselves with the causes, but the fact that the record is fragmentary and biased has a strong influence on the study of paleontology, particularly of the vertebrates, and on the role of museum collections in this study.

In practice there are two vertebrate paleontologies, one concerned with animals which have lived since the end of the Mesozoic Era, and the other with animals that became extinct before that time. The difference between the two is determined by three factors, one biological, the degree of similarity of the organisms to living forms, and a second geological, the degree of similarity of past to present physical circumstances of the earth's surface. The third factor, completeness of the record, is a product of both biological and geological influences.

The Cenozoic Era, the approximately 70 million years that have elapsed since the end of the Mesozoic, is often called the Age of Mammals, in reference to the fact that the dominant terrestrial vertebrates of this interval are mammals very similar in general to living forms. Lineages of the major orders of living mammals can be traced with a high degree of confidence in the changing faunas of the Cenozoic. The younger the faunas in question, the more directly can their components be compared with living animals, and although this comparison becomes somewhat more difficult as one goes back in time, the mammals of even the earliest Cenozoic are sufficiently similar to those of the present day to afford a basis for direct comparison. This is also true of Cenozoic amphibians (frogs and salamanders) and reptiles (crocodilians, lizards and snakes, turtles, and scattered relatives of *Sphenodon*).

Terrestrial vertebrate faunas prior to the Cenozoic were dominated by reptiles, most of the Mesozoic by dinosaurs, and the late Paleozoic and earliest Mesozoic by synapsid, or mammallike reptiles. Each of these groups was preeminent for about 130 million years, almost twice as long as the mammals have thus far enjoyed their supremacy. The most striking characteristic of these animals is the difference between them and the reptiles—or anything else—living today. Dinosaurs are often compared with birds, to which they are closely related, and synapsids can be compared with their descendants the mammals, or with unrelated reptiles such as turtles, with which they have many habitus features in common. But this is a far cry from comparing an early Cenozoic horse with *Equus*, or a Miocene arctoid carnivore with living dogs or bears. No terrestrial tetrapod of the present is closely comparable to either dinosaurs or synapsids in its general organization, in the way it makes its living. As a consequence, one is restricted to methods of classic comparative anatomy in working out relationships of pre-Cenozoic tetrapods, and resolution of all problems, whether taxonomic or functional, must be based for the most part upon the remains themselves, with only peripheral or analogical reference to living animals.

Geological aspects of Cenozoic time are similarly much more nearly comparable to present-day conditions than are those of earlier time. The major subdivisions of the fossil record, the Paleozoic, Mesozoic, and Cenozoic Eras, are related in some degree to long-term phases of mountain-building (tectonic cycles) over large parts of the earth. The cycle in which we find ourselves today was initiated at the beginning of the

Cenozoic and is still active. It has molded and continues to mold the general configuration of land masses (including major topography and drainage), and in doing so controls deposition of sediments and preservation of fossils.

Presumably the tectonic cycles of the Paleozoic and Mesozoic exercised the same influence over physical conditions on continental surfaces and over preservation of the faunas of those times. But the earth movements of each tectonic cycle result in the destruction of large parts of the features formed during preceding cycles, and in consequence much of the Paleozoic and Mesozoic record has been lost. Because present-day tectonics are essentially a continuation of the Cenozoic cycle, a far larger proportion of the Cenozoic terrestrial fauna is still preserved and exposed on the surfaces of all continents except Antarctica and perhaps Australia. Cenozoic faunas therefore tend in general to be more nearly complete and continuous than those of earlier time.

Destruction is selective. The higher the land, the more quickly it is eroded, and upland faunas are therefore rare even in the Cenozoic, except in its most recent phases. With a few notable exceptions, upland faunas are unknown in the Paleozoic and Mesozoic.

Tectonic activity of the current cycle has broken up the record of earlier eras both temporally and geographically. Except for bits and pieces, the long history of the dinosaurs is adduced from three segments of time totalling a good deal less than half their overall record. The earliest segment is that of the Upper Triassic, of perhaps 5 million years' duration, best represented in South Africa, Brazil and Argentina, western United States, and western Europe. The second segment, straddling the boundary between Jurassic and Cretaceous, lasted no more than 15 million years and perhaps as little as 5 million, and is best represented in western United States, western Europe, and Tanzania. The third segment is that of the Upper Cretaceous, of about 30 million years' duration, best represented in western United States and Outer Mongolia.

The history of synapsid reptiles as such (omitting Mesozoic mammals) extends essentially from the origin of reptiles some-time in the early Pennsylvanian to the end of the Triassic. The record is perhaps more nearly continuous temporally than that of the dinosaurs, but is sharply broken geographically. Approximately the first half, to the end of the Lower Permian, is best represented in the United States, while the second half is preserved in Russia, South Africa, Zambia, and Tanzania, and Brazil and Argentina.

The general effect of the characteristics of Cenozoic tetrapods and their record is to permit taxonomy and faunistics of the organisms to be studied in considerable detail. Species populations can often be recognized on the basis of preserved material, and confirmed, at least by analogy, by comparison with living populations. At higher stratigraphic levels, studies of rates of origin and longevity of genera and species in terms of absolute time are possible. In general, the most significant taxonomic work is concentrated below the level of order. Because of the relatively continuous record, studies of distribution are more meaningful, and the question of past migration can be approached directly. The occasional presence of such paleontological exotica as upland faunas gives students of this time period a better perspective for explicitly ecological faunal studies. Around its periphery, vertebrate paleontology of the Cenozoic merges imperceptibly into the more strictly biological disciplines of mammalogy and herpetology.

Few of these approaches are effective in the study of pre-Cenozoic tetrapods. Disjunction of the record makes questions of distribution and migration almost meaningless, for although we know where the animals were, we can never be sure of where they weren't. Because dinosaurs and synapsid reptiles are so different from living animals in morphology and biological requirements, and because we cannot be confident that the natural sampling of fossilization has preserved biologically relevant populations, in most cases we cannot confidently recognize reproductively isolated natural populations in the fossil material. Species designations are used to keep the picture consistent with neozoological practice, but in general the lowest operational taxonomic unit appears to correspond most closely to the genus of neozoology. Much of the significant work is concentrated at about the level of subclass.

Study of Paleozoic and Mesozoic vertebrates is therefore broad-brush paleontology. Although its low-level taxonomy is shaky, it provides an overall view of vertebrate evolution which since Darwin's time has gone far to document true relationships between vertebrate classes. Another approach, which has become more feasible in recent years as more material has become available, is the study of the functional anatomy of these outlandish beasts, which ultimately may provide insight into the selective forces that produced differentiation to such a high taxonomic level. Vertebrate paleontology of the Paleozoic and Mesozoic draws most heavily from comparative anatomy among the strictly biological disciplines, both in the classic approach and (by analogy) in studies of function.

The value of museum collections to vertebrate paleontology of whatever period is directly related to the fragmented quality of the record, for we can never predict what unprepossessing scrap of a fossil will next fill a gap in our knowledge. For Cenozoic specialists, identifiable bits often provide valuable data extending temporal or geographic range of mammal species. Fragments of crocodilians, turtles, and lizards identifiable no more closely than to subclass may contribute to the understanding of past climatic conditions, for these reptiles were presumably more restricted than mammals by climatic requirements. For the student of dinosaurs or synapsids, bits and pieces of ear, braincase, or jaw have contributed to resolution of problems of function and of high-level taxonomic relationships. This principle is also valid, of course, with respect to continuing field programs. One can predict only very generally what he will find in a given area, and it is only by sustained methodical collecting that these unexpectedly valuable pieces of the jigsaw puzzle accumulate.

In spite of its incompleteness, the fossil record is so enormous that no single institution can hope to cover more than a small part of it comprehensively, and few institutions are large enough to have a completely representative collection in all areas. Economic factors dictate that most museums that include vertebrate fossils concentrate on a more or less regional coverage. As a consequence, collections themselves represent additional fragmentation of available material.

The reason that vertebrate paleontology has been so successful in piecing together the torn-up manuscript with which it must work is that the material has in fact been available, if scattered. Great strides have recently been made in the interesting transitional areas between amphibians and reptiles, and between reptiles and mammals. Although both were triggered by discovery of new specimens, both were properly consolidated and documented by exhaustive reexamination of old material, some of it having been available for about 150 years. These developments have stimulated activity in these and related areas, and more information may be expected momentarily, but if the potential of this sort of work is to be realized, collections must remain readily available. The question is not only how to make room for new and significant material, but how to do this and at the same time keep existing collections efficiently accessible.

A final point to emphasize is that for the decipherment of the morphology and general organization of extinct vertebrates, paleontologists are restricted to a single organ system, the skeleton. Fortunately, the vertebrate skeleton is biologically plastic, and readily reflects the former presence of many soft parts, as well as certain aspects of growth and development. But in order to interpret these features effectively, the vertebrate paleontologist is very dependent upon collections of preserved specimens of present-day animals. For some problems, such as direct comparison of populations, he requires skeletons or suites of skeletons. For others, such as those involving comparative anatomy, he requires alcoholic specimens for detailed dissection. In summary, then, because of the incompleteness of primary materials, the continuing effectiveness of vertebrate paleontology requires that as much material as possible be available, not only fossils, but also relevant Recent specimens. In this field it is possible, in large measure, to compensate for the lack of what we can't get by accumulating an abundance of what we can.